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The neural correlates of perceiving human bodies: an ERP study on the body-inversion effect

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The present study investigated the neural correlates of perceiving human bodies. Focussing on the N170 as an index of structural encoding, we recorded event-related potentials (ERPs) to images of bodies and faces (either neutral or expressing fear) and objects, while subjects viewed the stimuli presented either upright or inverted. The N170 was enhanced and delayed to inverted bodies and faces, but not to objects. The emotional content of faces affected the left N170, the occipito-parietal P2, and the fronto-

central N2, whereas body expressions affected the frontal vertex positive potential (VPP) and a sustained fronto-central negativity (300–500 ms). Our results indicate that, like faces, bodies are processed configurally, and that within each category qualitative differences are observed for emotional as opposed to neutral images. *NeuroReport* 15:777–780 © 2004 Lippincott Williams & Wilkins.

Key words: Emotional processing; Event-related potentials; Face perception; Inversion effect; N170; Whole body perception

INTRODUCTION

The human body is a precious tool for achieving a large array of goals and, at the same time, a unique medium of emotional expression. For example, as was noted by Charles Darwin, and illustrated by ethologists, movements and postures of the whole body are potent cues for rapid communication of emotional states. So far, the study of emotional communication in humans has been largely confined to the study of isolated facial expressions. A central theme in face perception research concerns the issue of whether there are specialized processing routines for faces. The role of a configural processing routine is a fundamental issue in these debates. Studies suggesting that perceptual routines for faces are different from those used for recognition of non-face objects maintain that faces are recognized based on information provided by the overall configuration in which the facial parts occur, whereas recognition of non-face objects relies at least as much on recognition of isolated parts [1]. The most important source of evidence for the configural processing hypothesis comes from studies on the so-called face-inversion effect, which refers to the classical finding that face recognition is impaired if faces are presented upside down [2]. Recognition is disrupted much more for faces than for objects and this is manifested in a face-sensitive ERP (event-related potential) component called the N170. The N170 is a negative brain potential peaking at about 170 ms after stimulus onset at the lateral occipito-temporal sites. Typically, the N170 to inverted faces is larger and more delayed than the N170 to upright faces, but not than that to inverted objects [3]. The standard explanation of the face-inversion effect is that inverted faces disrupt the processing of

configural information [3,4]. The notion that configural processing as indexed by the inversion effect is unique to faces was, however, challenged by a study [5] that demonstrated the inversion effect for whole human body postures, indicating that, like faces, bodies seem to be processed configurally as well.

Against this background, an interesting issue is whether perceiving whole body images will also elicit the N170 and whether stimulus inversion is reflected in the N170. Therefore, the primary aim of the present study was to investigate the body-inversion effect using the face-specific N170. A second aim was to test whether the difference between emotional body expressions as compared to meaningful but neutral body images is reflected in the ERP. We know that certain ERP components are sensitive to different facial expressions [6,7], yet no study has examined this for body expressions. There is reason to expect that modulation of body expressions can be studied at an electrophysiological level. A recent brain imaging study [8] showed that body expressions of fear activate the amygdala, a brain area that has been associated with the processing of fearful faces. In the current experiment, we compared the inversion effect between faces, bodies, and objects. ERPs elicited by emotion (fear *vs* neutral) were studied in faces and bodies.

MATERIALS AND METHODS

Participants: Twelve healthy participants (18–26 years, mean 21.4 years) with normal or corrected-to-normal vision volunteered to take part in the experiment.

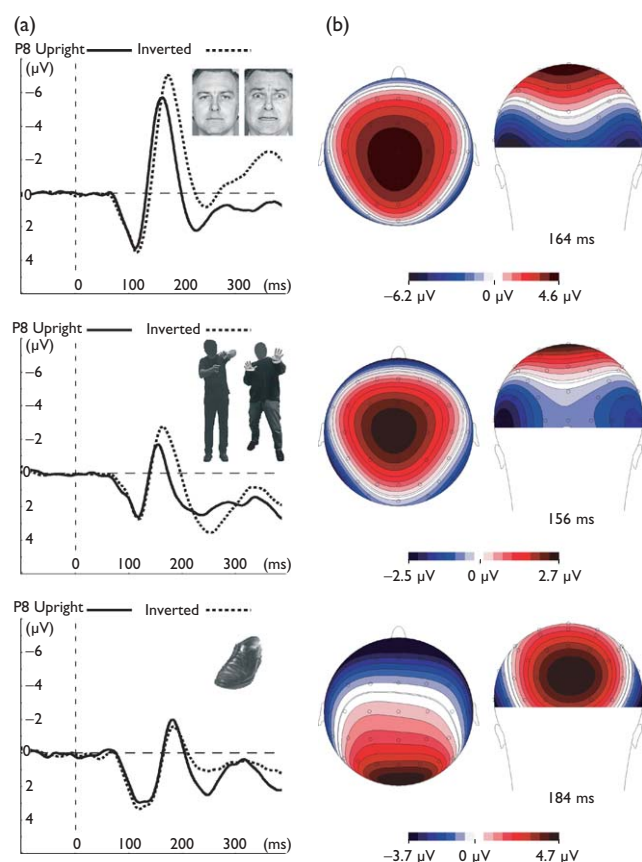


Fig. 1. (a) Grand-averaged ERPs at P8 to upright (solid line) and inverted (dotted line) faces (top), bodies (middle), and objects (bottom). (b) Scalp distribution of peak amplitude of the N170 to upright stimulus presentations. ERPs and topographies of faces and bodies were pooled across emotion (neutral, fear).

Stimuli and procedure: Photographs were taken from whole bodies of six males and six females [8] (Fig. 1) who adopted a fearful posture and a neutral posture (by performing a simple action such as pouring water in a glass, combing hair, putting on trousers, and opening a door). To minimize face processing during presentation of bodies, the faces on the photographs were masked with an opaque gray patch. Neutral and fear face stimuli were pictures of 12 individuals (six males, six females) taken from a validated image database [9]. Pictures of objects were photographs taken of six different shoes in upper front view at three-quarters orientation. The subtended viewing angle of the stimuli ranged from 9.6–10° vertical and 3.4–7.9° horizontal. Stimuli were presented for 500 ms. The experiment comprised three blocks (240 trials per block). Each block contained either bodies, faces, or objects. Half of the stimuli were presented upright while the other half was presented at an inverted position. Within the upright and inverted stimulus categories, half of the face and body stimuli were neutral, whereas the other half was fearful. Trials were randomly presented. The order of blocks was quasi-randomized across participants. Each stimulus was immediately followed by a central fixation cross, lasting 500–1500 ms. The participant's task was to decide whether the stimulus was presented upright or inverted using two designated buttons, which had to be pressed after termina-

tion of the fixation cross. A delayed response was given to lower the risk of the ERPs being contaminated by motor activity. The next stimulus followed at 1500 ms after the response.

ERP recording and analysis: EEGs were recorded from 49 locations using active Ag–AgCl electrodes (BioSemi Active 2) mounted in an elastic cap, referenced to an additional active electrode (Common Mode Sense) during recording. EEG signals were band-pass filtered (0.1–30 Hz, 24 dB/octave) at a sample rate of 256 Hz and off-line referenced to an averaged reference. Horizontal EOGs were recorded from two electrodes placed at the outer canthi of both eyes. Vertical EOGs were recorded from electrodes on the infraorbital and supraorbital regions of the right eye in line with the pupil. The raw data were segmented into epochs of 800 ms, including a 100 ms prestimulus baseline. After EOG correction, epochs with an amplitude change exceeding $\pm 100 \mu\text{V}$ at any channel were automatically rejected. ERPs were averaged separately for all stimulus categories (for faces and bodies: upright neutral, upright fear, inverted neutral, inverted fear, for objects: inverted and upright). We first analyzed the characteristics of N170 and its positive counterpart (vertex positive potential, VPP) elicited by bodies, faces, and objects. The N170 was scored at occipito-temporal sites as the maximal negative value in a window of 140–200 ms post-stimulus relative to mean pre-stimulus baseline. The VPP was scored as the maximal positive amplitude at the midline electrodes Fz, FCz, Cz, CPz, and Pz using the same time window. Analysis of the inversion effect was confined to the electrode positions at which the inversion effect is most pronounced (P7 and P8) [3]. To investigate the effect of emotional expression additional peaks were scored, that is, P2 at occipito-parietal and N2 at fronto-central sites in a 200–300 ms time window. Separate multivariate analyses for repeated measures were performed to analyze the effects.

RESULTS

Performance on the forced-choice task (upright *vs* inverted) during measurement was nearly flawless (99.8% correct). After completion of the experiment, we tested whether fear bodies were indeed perceived as having a fearful expression. Participants rated the pictures of the bodies by indicating either a fearful expression or one of the four neutral expressions. In 83% of the cases fearful bodies were correctly identified.

Figure 1a shows the N170 at P8 to upright and inverted faces, bodies, and objects. Peak amplitude N170 to upright stimuli (for faces and bodies collapsed across emotion) differed between the stimulus categories ($F(2,10)=30.26$, $p < 0.001$). N170 amplitude did not differ significantly between hemispheres for all stimulus categories. N170 amplitude for faces was significantly larger than for bodies ($F(1,11)=58.01$, $p < 0.001$) and objects ($F(1,11)=41.74$, $p < 0.001$) whereas N170 amplitude for bodies did not significantly differ from objects ($F < 1$). Peak latency of N170 also differed significantly between categories (faces 167 ms, bodies 157 ms, and objects 182 ms; $F(2,10)=30.30$, $p < 0.001$). N170 latency was longest for objects compared to faces and bodies ($F(1,11)=13.92$, $p < 0.001$; $F(1,11)=61.76$, $p < 0.001$, respectively). N170 latency for bodies was

significantly earlier than for faces ($F(1,11)=9.94$, $p < 0.01$). In Fig. 1b, the scalp distribution of the N170/VPP complex is illustrated. As is evident from Fig. 1b, the topography of N170/VPP for faces and bodies was very similar and different from what is observed for objects. To test the topographic difference between stimulus categories, amplitudes for the leads under consideration were vector-normalized to eliminate the risk of topography differences being confounded by amplitude differences [10]. Topography of N170 was tested at the leads surrounding P7/P8 (P7/P8, CP5/6, TP7/8, P5/6, PO3/4, and PO7/8). There was no interaction between lead and stimulus, indicating no significant difference in topography of N170 between faces, bodies, and objects. Scalp distribution of VPP amplitude at the midline leads (Fz, FCz, Cz, CPz, and Pz) differed between stimulus categories ($F(8,4)=36.79$, $p < 0.01$). Simple effect tests of VPP topography revealed no differences between faces and bodies ($F < 1$). VPP topography of objects differed significantly from that of faces ($F(8,4)=23.11$, $p < 0.001$) and bodies ($F(8,4)=12.86$, $p < 0.01$). As shown in Fig. 1b, VPP was maximal at Cz for faces and bodies, for objects VPP was maximal at POz.

Fig. 1a indicates an inversion effect for faces and bodies but not for objects. Inverted faces and bodies elicited enhanced N170 amplitudes compared to upright faces and bodies ($F(1,11)=9.42$, $p < 0.05$; $F(1,11)=6.08$, $p < 0.05$, respectively). N170 was delayed for faces (12 ms; $F(1,11)=76.42$, $p < 0.001$) and bodies (12 ms; $F(1,11)=17.70$, $p < 0.01$). The inversion effect on peak amplitude and latency did not significantly differ between faces and bodies. No inversion effect on N170 amplitude and latency was found for objects ($F < 1$).

The effect of emotional expression in upright faces and bodies is shown in Fig. 2. Testing N170 for faces at P7/8 revealed an interaction between emotion and lead ($F(1,11)=6.60$, $p < 0.05$). Fear faces elicited a more negative N170 than neutral faces at P7 ($F(1,11)=19.07$, $p < 0.01$) whereas no effect of emotion was found at P8. Facial expression had its largest effect at about 230–250 ms, manifested in a lateral occipito-parietal P2 and a centro-frontal N2. Neutral faces elicited a more positive P2 ($F(1,11)=14.92$, $p < 0.01$) and a more negative N2 compared to fearful faces ($F(1,11)=8.71$, $p < 0.05$). Visual inspection of Fig. 2 indicates that body expression had a different effect on the ERP than face expression. N170, N2, and P2 amplitudes were unaffected by expression. However, an early effect (152 ms) of expression was found on VPP amplitude at the frontal leads, with larger amplitudes for fear bodies than for neutral bodies ($F(1,11)=6.20$, $p < 0.05$) whereas for faces VPP was not different between neutral and fear expressions ($F < 1$). At the fronto-central midline area, bodies elicited a sustained negativity starting after N2, which was enhanced for fear expressions compared to neutral ones. This observation was substantiated by testing the mean amplitude values in a 300–500 ms interval at FCz ($F(1,11)=5.14$, $p < 0.05$).

DISCUSSION

We investigated the neural correlates of the perception of human bodies and focussed on whether viewing images of human bodies elicited an N170 and whether this would be different for upright *vs* inverted stimuli as previously found for faces. We found a larger N170 amplitude for faces than

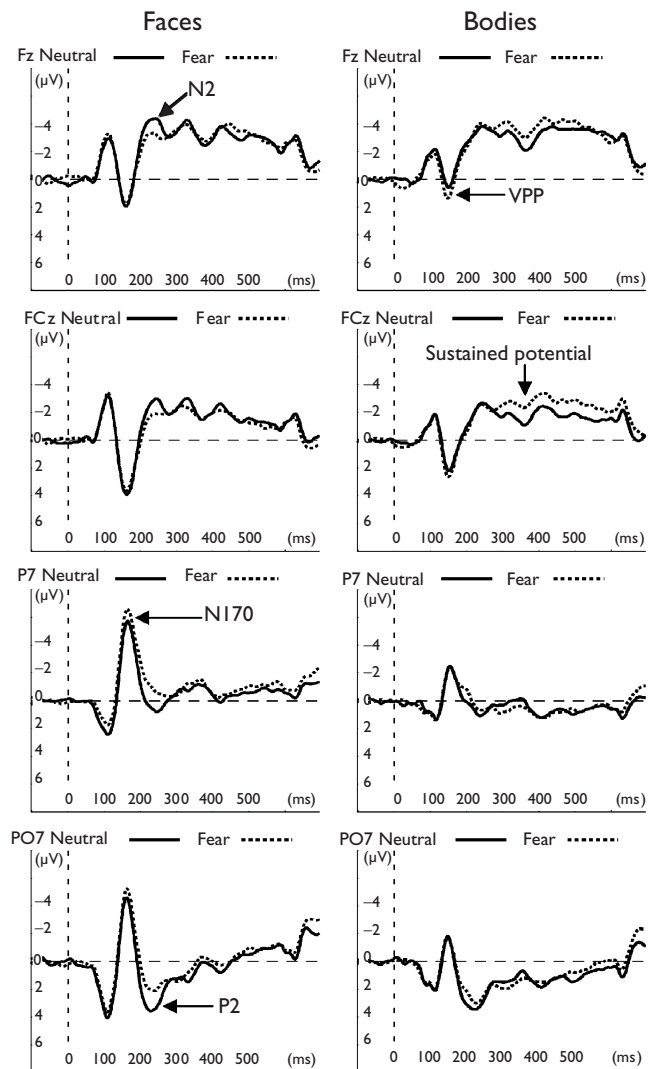


Fig. 2. Grand-averaged ERPs elicited by upright fear (dotted line) and upright neutral (solid line) faces (left) and bodies (right).

for bodies and objects. This, however, does not provide decisive evidence in favor of face specificity. Amplitude differences may be the result of low-level visual differences between stimulus categories [3]. Furthermore, in the present experiment the topography of N170/VPP for faces and bodies was much alike, but significantly different from objects. More important, to both inverted faces and bodies the N170 was equally enhanced and delayed, while no effects were found for inverted objects. This result supports the notion that there are important similarities between encoding of faces and bodies, as was also suggested by reports on the body-inversion effect at the behavioral level [5]. The fact that the scalp distribution of N170 and the inversion effect of N170 for faces and bodies are very similar suggests that the N170 can be considered a marker of an early structural encoding stage in the perception of both faces and bodies. Our data are consistent with the notion that the N170 is associated with a mechanism that triggers configural processing in the fusiform cortex [11]. Our data also support the finding of a complete overlap of processing of faces and body expressions in the fusiform cortex [8].

We used images of body expressions without any information about facial expression. Nevertheless, one might argue that the brain fills in the appropriate missing face expression by using mental imagery and semantic knowledge. In our view, though, such semantic processes are unlikely to explain the present data. Ganis and Kutas [12] have shown that this mental imagery is associated with a time window of around 400 ms, which is much later than the time window associated with a structural encoding stage (around 170 ms).

Our results have implications for a better understanding of the category specificity of the N170. In the face-perception literature it has been questioned whether the N170 is face specific. The present results suggest a broader functional significance of the N170, which could include holistic perception of faces and bodies alike. Considering the evolutionary importance of adequate recognition of both face expressions and body language, one may conjecture that our proficiency in these two domains has a similar origin.

Our second aim was to investigate the visual processing of emotional expression in bodies. Emotional processing of body expressions differed qualitatively from that of faces. Although emotional processing was initiated at approximately the same time, the locus of this effect differed between faces (left-sided occipito-temporal N170) and bodies (VPP at the frontal sites). The second ERP deflection that was sensitive to emotional content in faces was the occipito-parietal P2 and the fronto-central N2. It is generally agreed that these peaks are related to the decoding of facial expressions [6,7]. Body expressions, however, had no effect on these components but did affect a sustained fronto-central potential at a longer latency. The sustained effect of bodies with fearful expression may reflect prolonged attention to emotionally relevant stimuli. This cannot be explained by low-level differences between fear and neutral bodies because, when additionally tested, no effect of emotion was found for inverted bodies. At present we can only speculate why the pattern of ERP modulation induced by emotional expression differs between faces and bodies. It may be argued that bodies without faces provide a weaker cue about the emotion being conveyed than face expression, leaving the perceived status of body expressions more ambiguous. The ambiguity of body expressions may explain the sustained potential for fearful bodies. Whereas face expressions are recognized automatically at an early stage [6,7], processing of body expression might be prolonged because of the perceived ambiguity in body expression.

Further research needs to address the extent to which perception of bodies and faces recruits the same cognitive mechanisms as both categories provide similar socially relevant signals, such as gender, age, intentions, and emotions.

To conclude, configural processing of bodies, as reflected by the N170 inversion effect, strongly resembles the configural processing of faces suggesting that humans have developed a natural recognition ability for both faces and bodies. However, when an emotional component was present we observed differences between faces and bodies. This suggests a possible dissociation between similarities in structural encoding of faces and bodies on the one hand and emotional encoding of faces and bodies on the other. In this study, participants performed an orientation detection task (upright *vs* inverted), selected because it directs attention away from the emotional content of the stimuli. Future research will need to address how brain potentials are affected by body expressions if attention is focused on the emotional content.

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